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FEEDING PATTERNS OF THE LONG-FINNED SQUID, *LOLIGO PEALEI,* IN NEW ENGLAND WATERS

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Abstract

Gut content analyses have shown that the diet of the long-finned squid, *Loligo pealei*, differs between inshore spawning and nursery grounds and offshore winter grounds. In this study, squid were collected inshore from May through November in lower Narragansett Bay, Rhode Island and offshore during winter along the continental shelf between Cape Hatteras and Cap Cod. In both collections crustaceans were more frequently consumed than either fish or squid, but fish were eaten by a wider size range of squid and more frequently inshore. Prey-type selection based on size was common in both samples, but it is unlikely that the species composition is the same in both areas. These data suggest that *L. pealei* is a highly opportunistic predator, whose diet primarily reflects the local abundance of potential prey species. Such a flexible feeding strategy could account for the large spatial and temporal variations which have been reported in the diet of this squid from various offshore areas.

Introduction

Studies of the trophic dynamics of the California squid, *Loligo opalescens* (Morejohn *et al.*, 1978), clearly indicate the central role of this intermediate predator in coastal food webs. Squid are important because they both compete with and serve as prey for higher carnivores, and thus must be carefully considered when developing multispecies fishery management strategies (May *et al.*, 1979). Comprehensive studies of the trophic dynamics of *Loligo pealei*, the common squid of New England, have not yet been reported. In spite of the fact that *L. pealei* is an important food source for many commercially important fish, both inshore and offshore (Verrill, 1882; Tibbetts, 1975, 1977), details of its own feeding dynamics while inshore are generally lacking. However, weakfish (*Cynoscion regalis*) and scup (*Stenotomus crysops*) have been reported in the stomachs of *L. pealei* (Oviatt and Nixon, 1973) from Narragansett Bay, and squid have been directly observed feeding upon menhaden and sculpin (*Brevoortia tyrannis* and *Myxocephalus* sp., H. W. Pratt, NMFS, personal communication), sand lances (*Ammodytes americanus*, Caroline Griswold, NMFS, personal communication), silversides, mummichogs, anchovies, and grass shrimp (*Menidia menidia, Fundulus* spp., *Anchoa mitchili*, and *Palaemonetes* spp., author).

Studies of the offshore feeding habits of *Loligo pealei* (Vovk, 1972, 1974; Vinogradov and Noskov, 1979) indicate that feeding activity varies diurnally and seasonally, and that the relative importance of crustaceans, fish, and other squid in the diet varies with the size of the squid. The broad latitudinal and depth ranges of this species may be expected to be reflected in the diets of squid from different areas as well. *L. pealei* is continuously distributed from the coast of Columbia to

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Nova Scotia (Cohen, 1976). In the northern half of its range at least (Cape Hatteras through New England), *L. pealei* overwinters on the continental shelf and slope at depths to over 200 m (Summers, 1969; Vovk, 1978) and migrates in late spring and early summer into shallow coastal spawning areas (Verrill, 1882; Haefner, 1964; Summers, 1968, 1971; Macy, 1980).

The goals of this study were therefore to first determine the composition of the inshore diet of *Loligo pealei*, and to then interpret the results in light of our current understanding of the basic life history patterns and strategies of this and other similar squid species.

Materials and Methods

Details of the sampling procedure and sampling dates will be briefly outlined here since they have been reported elsewhere (Macy, 1980, 1982). Samples of approximately 100 squid each were collected at two-week intervals from late April through November, 1978 (inshore samples) in lower Narragansett Bay, Rhode Island, U. S. A. Three additional samples, taken during early and late winter (R/V Cryos, 1976 and R/V Argus, 1977, 1978) on the continental shelf (offshore samples), were also provided by the National Marine Fisheries Service, Woods Hole, Massachusetts. Since specialized knowledge is required to taxonomically classify prey items on the basis of the small fragments found in squid stomachs (Bidder, 1950; Karpov and Cailliet, 1978), squid gut contents were only grossly categorized on the basis of appearance as "crustaceans", "squid", "fish", "algae", "unknown", and combinations of the first three groups. Since all samples were taken without regards to time during the daylight hours, generally in mid-morning for the inshore samples, no attempts were made to correlate feeding patterns with time of day. Mantle length, sex, and stage of maturity were recorded, however, to allow analysis of possible sex or size related food preferences. Insights into the actual feeding behavior were obtained from direct observations of squid under natural and laboratory conditions.

Results

Slightly over 50% of inshore and offshore squid had empty guts (Table I), but no obvious relationship between size of the squid (mantle length, ML) and the presence or absence of food could be detected. The extreme ranges of mantle lengths were similar in both collections, from 1–34 cm inshore (Fig. 1a) and 3–29 cm offshore (Fig. 2a), but the modal sizes differed considerably. The modal length of the inshore samples was about 5 cm, primarily reflecting the presence of large numbers of young of the year, while offshore squid were larger with a modal length of about 10 cm. With respect to prey composition, crustaceans, squid, and fish accounted for over 80% of the total stomach contents in both collections (81.9% and 86.3%, Table I), on a frequency of occurrence basis. While the relative importance of crustaceans in the diet was also similar between samples, 58% inshore and 49% offshore (Table I), the importance of fish and squid did differ. Inshore, fish ranked second in importance at 17%, followed by squid in 11% of the guts. In the offshore samples, squid ranked second at 20%, with fish third at 12%. Unidentified matter amounted to about 10% in both samples, and in four inshore squid small amounts of green algae were found. Since squid are carnivores, the incidence of plant matter in the guts must be considered spurious (see Vovk, 1972, and Stunkard, 1977 for other records of algae).

TABLE I

Stomach contents by frequency of occurrence of prey in pooled 1976 R/V Cryos and 1977–78 R/V Argus (offshore) and 1978 Narragansett Bay (inshore collections). Of a total of 3875 inshore squid, 2667 were examined for stomach contents. F = fish; C = crustaceans; S = squid.

	Offshore		Inshore	
Food	Frequency	% With food	Frequency	% With food
Empty	465		1419	
Crustaceans	191	49.48	724	58.01
Squid	79	20.47	139	11.14
Fish	46	11.92	214	17.15
F & C	13	3.37	16	1.28
S & C	8	2.07	16	1.28
S & F	5	1.30	13	1.04
Algae	0	0.0	4	0.32
Unknown	44	11.40	122	9.78
Total	851	100.01	2667	100.00
With Food	386	45.4	1248	46.79

The data presented in Figures 1b and 2b also show that food type varies with the size of the squid. Crustaceans were most frequently eaten by squid 9 cm ML or smaller in the inshore samples and by those less than 14 cm ML from offshore. Squid and fish both seem to be eaten by all but the smallest squid from both areas, but were the dominant food (present in greater than 50% of the food-containing guts) in only the larger squid. In the inshore samples (Fig. 1b) fish became most important in squid 11 cm and larger (60% of those with food), but in the offshore samples (Fig. 2b), squid or fish were not dominant until squid reached sizes of 16 cm (66.7%) and larger. There also appears to be a tendency for those squid from offshore to feed less on a single food type than do their inshore counterparts. The narrow peaks of fish and squid consumption in both collections (Fig. 1b and 2b) are artifacts of small sample size in the larger squid size classes.

Observations of feeding activities and behavior of wild and captive squid (Macy, 1980) provided another source of information. Long-term observations of captive squid revealed that a behavior pattern described by Williams (1909, cited by Bidder, 1950) and Stevenson (1934) in conjunction with feeding and spawning activities, respectively, is actually quite common at all times, particularly during periods of bright illumination. The behavior seems to represent a resting posture, in which the squid lie on the bottom with their posterior ends and tips of the arms in contact with the substrate, when resting, waiting for prey, and eating. Typically the squid also assume a transversely banded cryptic coloration pattern, which blends well with a mottled substrate of rocks, pebbles, sand, and algae. Wild squid have been frequently seen resting on the bottom, and on occasion they have been seen dropping to the bottom to avoid large predators such as striped bass (*Morone saxatilis*) (H. W. Pratt, NMFS, Narragansett, personal communication). With regards to the prey of squid, adults 15 cm ML and larger have been observed feeding eagerly on small shrimp (*Palaemonetes* and *Crangon*) which they picked individually from the bottom, as well as on much larger prey such as menhaden nearly one-half their own length (see Macy, 1980, Fig. 34).

Prey attributes other than size alone may be important also. In the laboratory, spiny fish such as sticklebacks (*Apeltes* and *Pungitius*) were captured but rejected,

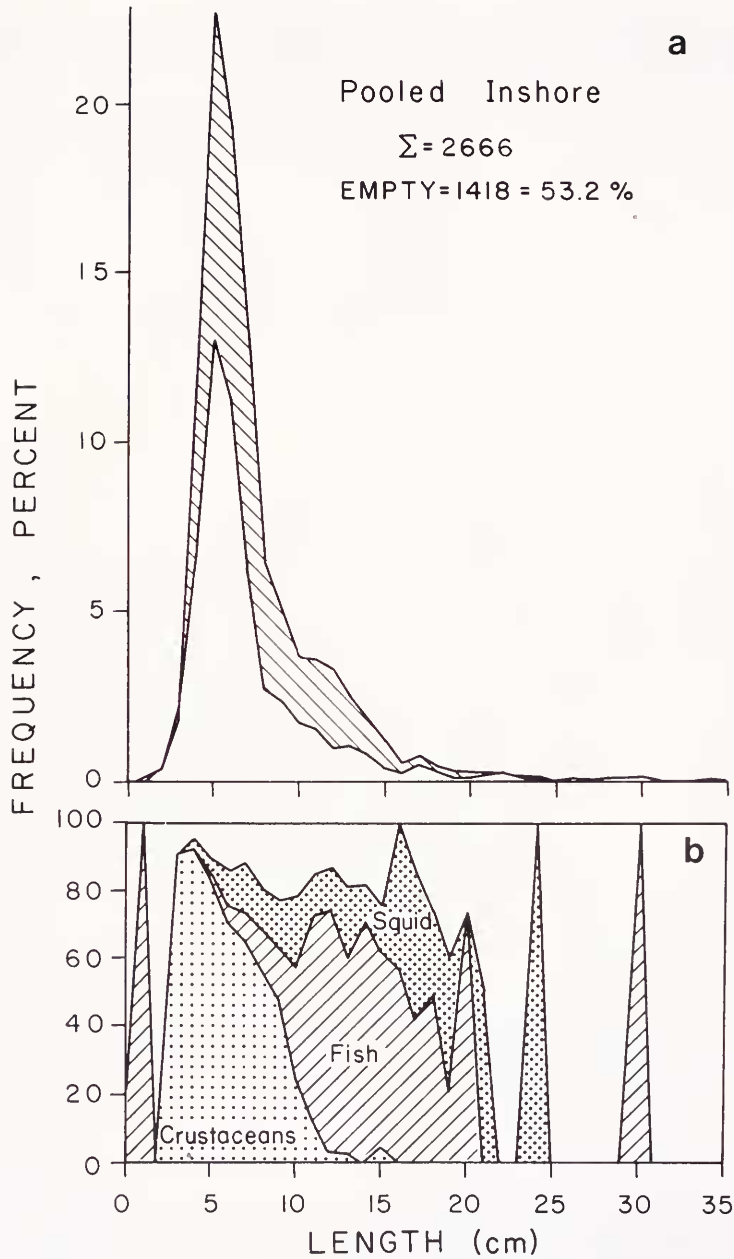

FIGURE 1. Size distribution of squid containing food (cross-hatching in a.) and the distribution of major prey categories as a function of the size of squid (b) from the pooled Narragansett Bay collections. The unhatched area in (a) represents squid without food.

while other species such as striped mummichogs (*Fundulus majalis*) appeared to be difficult to successfully subdue. When fed individuals of this species larger than about 50 mm fork length, even large squid (greater than 15 cm ML) frequently

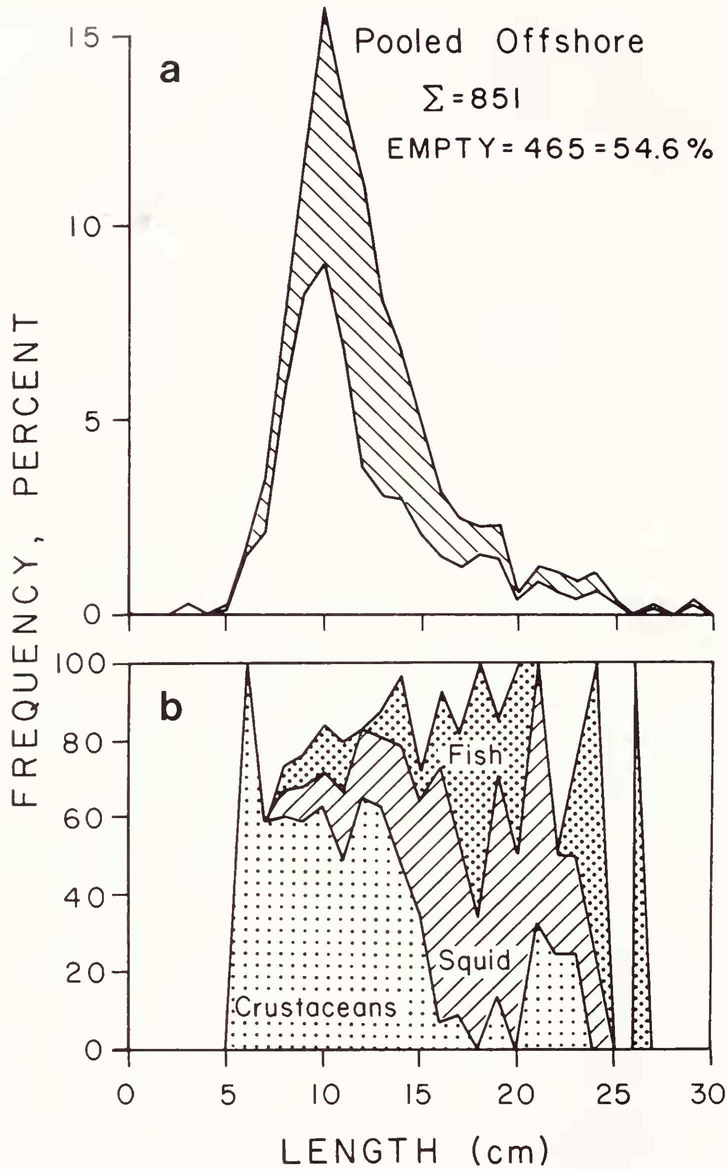

FIGURE 2. Size distribution of squid containing food (a) and the distribution of major prey categories as a function of the size of the squid (b) from the pooled offshore collections.

damaged the tips of their arms and tentacles. Aside from such problem fish, captive squid successfully attacked and ate a wide variety of fish of the genera *Anchoa, Menidia, Fundulus, Cyprinodon, Ammodytes, Brevoortia,* and even *Anguilla,* provided that they were no larger than perhaps 30% of the squid's mantle length.

Parasitism of squid by the tetraphyllidean cestode, *Phyllobothrium lologinis* Linton, 1907, whose intermediate host is thought to be a copepod (Stunkard, 1977) was evident in the early summer inshore samples. Most frequently the parasites were observed in the caeca and stomachs of the squid, but occasionally individuals were found unattached in the mantle cavity or emerging from the anus. Typically 1–2 parasites were observed per squid (up to 6 on occasion), but only the larger squid were infected: 2 parasitized squid less than 10 cm mantle length were seen. A clear seasonal pattern of infection was evident. In the May 31 sample, 40% of the squid were infected, but the rate had fallen to between 18 and 21% during the period between June 30 and July 17. By late July less than 5% of the inshore samples contained parasites, and rates remained practically nil for the remainder of the inshore season. No parasites were observed in the 102 squid from the November 1977 R/V Argus offshore sample, but 9 of the 151 squid from the March 1978 R/V Argus sample, all larger than 12 cm ML, were infected.

Discussion

Relative prey size

In general, the diets of inshore and offshore squid do not appear to differ greatly with respect to their gross prey composition. Crustaceans were found in 50% or more of the guts from both samples, and were nearly twice as important overall as fish and squid combined. Before these results can be compared with those of other studies, however, two points should be noted. First, various methods have been used to evaluate the importance of particular prey (Table II), and second, the size distribution of squid has not always been adequately accounted for. The latter point is especially important when comparing the diets of squid from different areas or seasons (Table II). The offshore data from this study ("pooled lengths," Table II) agree well with those of Vovk (1972) on a frequency of occurrence basis, but values expressed on a volume percent basis suggest that fish were more important overall than crustaceans. On a weight percent basis (Vinogradov and Noskov, 1979, Table II), fish appear to be still more important.

Food preferences based upon the relative sizes of predator and prey have been previously reported for *L. pealei* (Vovk, 1972), as well as for *L. opalescens* (Fields, 1965; Karpov and Cailliet, 1978) and *Illex illecebrosus* (Squires, 1957; Ennis and Collins, 1979; Vinogradov and Noskov, 1979; Amaratunga, 1980), and would be expected considering certain morphological changes which occur as squid grow. In loliginids at least, streamlining improves with growth (*i.e.,* increased length:width ratios) (Haefner, 1964; Macy, 1980), which allows higher pursuit speeds to be attained (Packard, 1969). Relative fin area also increases with length, which enhances mobility. In practice, however, the range of suitably-sized prey for a given squid appears to be quite large. Adult *L. pealei* have been observed eating small shrimp perhaps only one-twentieth of their mantle length, while Vovk (1972) found that fish as large as 19 cm may also be eaten. O'Dor *et al.* (1980) suggests that *I. illecebrosus* can successfully attack and subdue fish equal to their own mantle length. At the population level, both inshore and offshore samples revealed abrupt changes in prey preference as the squid grow. Inshore, the transition between crustaceans and fish occurred at about 9 cm mantle length, while offshore the shift from crustaceans to a mixed fish/squid diet occurred at about 15 cm mantle length. These findings also agree with those reported by Vovk (1972) for offshore areas. Size constraints are likely to be particularly important to hatchlings and young juveniles, however, because of their limited speed and mobility. Unfortunately, gut analyses for very small individuals are lacking at present.

TABLE II

Relative importance of prey items in the diet of Loligo, *based on gut content analyses.Legend: M.L. = dorsal mantle length; N.E. Shelf = New England continental shelf, Cape Hatteras to Cape Cod unless otherwise noted; Euph = euphausids; Cop = copepods.*

Location, month collected (source)	M.L., cm		*Crustaceans*	*Fish*	*Squid*
				% frequency	
Loligo pealei					
Narragansett Bay, V–IX (this study)	pooled		58.0	17.2	11.1
	3–15		59.0	16.4	10.5
	16–30		0.0	41.2	35.3
N.E. Shelf, XI–XII, III (this study)	pooled		49.5	11.9	20.5
	3–15		56.7	8.9	16.0
	16–30		10.0	45.0	28.3
X (Vovk, 1972)	pooled		44.9	21.1	26.6
				% total volume	
X? (Vovk, 1972)	pooled		37.1	38.4	18.6
				% total weight	
N.E. Shelf, VIII–IX (Vinogradov and Noskov, 1979)	pooled		20.4	53.4	26.2
Georges Bank, VIII	8–15		100.0	—	—
	16–30		65.0	32.0	3.0
Nantucket, VIII	8–15		55.0	13.0	32.0
So. of Long Island, IX	8–15		33.0	39.0	28.0
	16–30		17.0	47.0	36.0
Loligo opalescens		*"index of relative importance"*			
Monterey Bay, I–XII (Karpov and Cailliet, 1978)		*Euph.*	*Cop.*	*Fish*	*Squid*
Deep Water	pooled	6552.2	103.8	1.3	2.6
Shallow Water	pooled	1553.4	1.0	44.8	187.6
Spawning Grounds	pooled	0.0	0.0	11.3	0.0
Overall	2.1–10	3988.0	97.5	2.0	16.2
	10.1–18	5400.0	37.5	8.8	9.7

Prey availability

The wide geographic range of *L. pealei* should be reflected in the varying importance of given prey types in the diets of comparable sized squid from different locations. In the Narragansett Bay samples (Fig. 1b) squid of all sizes tended to feed on a single prey type, and few squid larger than 10 cm ML contained crustacean remains. In the offshore samples, however, a mixed diet was more evident (Fig. 2b) in the 12–25 cm size classes, and crustaceans were present in squid of all sizes. In August on Georges Bank (Vinogradov and Noskov, 1979) (Table II) 8–15 cm squid fed exclusively on crustaceans, while during September, south of Long Island, New York, the same size squid were feeding about equally on crustaceans, fish, and squid. In the colder, deeper waters euphausids are an important food for *L. pealei* (Vovk, 1972; Vinogradov and Noskov, 1979), as they also are for *L. opalescens* (Karpov and Cailliet, 1978) and *Illex illecebrosus* (Squires, 1957; Ennis and Collins, 1979; Amaratunga, 1980). Copepods, hyperiid amphipods, and mysid and pandalid shrimp may also be important. Myctophid fishes are heavily preyed upon in offshore waters (Vovk, 1972; Vinogradov and Noskov, 1979), but especially during fall large squid also feed on small silver hake (*Merluccius bilinearis*), while small squid and hake alike compete for fish, squid, shrimp, and euphausid resources (Vovk, 1975; Vinogradov and Noskov, 1979).

One may thus expect significant changes in the diet and perhaps even the feeding behavior to occur when squid move into the shallow inshore environment. The Narragansett Bay area is a particularly rich nursery ground for a wide variety of fish, many of which are abundant during the summer months when the squid are present (Tracy, 1905; Richards, 1963; Jeffries, 1968; Oviatt and Nixon, 1973; Saila and Pratt, 1973; Jeffries and Johnson, 1974). It is not, therefore, surprising that fish formed the bulk of the diet of squid as small as 10 cm there. Offshore, relatively large pelagic crustaceans such as euphausids and copepods (*Meganyctiphanes, Candacia, Calanus,* and *Centropages*) were the dominant prey of squid as large as 10–15 cm ML (Vovk, 1972; Vinogradov and Noskov, 1979), but these organisms are not generally abundant in Narragansett Bay. According to Jeffries and Johnson (1973), the local inshore zooplankton is dominated by relatively small copepods such as *Acartia, Temora, Pseudocalanus,* and *Centropages*. It is also evident from the incidence pattern of the copepod-carried parasite described previously (*e.g.* only large squid from offshore infected) that the unidentified host copepod must not be present in inshore waters either. Pelagic shrimps and other crustaceans may be replaced in importance inshore by demersal forms such as *Palaemonetes* and *Crangon* (Zinn, 1969; Oviatt and Nixon, 1973) and by a variety of larval and juvenile crabs which are also present (Hillman, 1964; Reilly, 1975; Oviatt and Nixon, 1973). Thus the availability of a large juvenile fish resource coupled with a lack of large pelagic crustaceans inshore can reasonably account for the prevalence of fish in the diets of a wider size range of squid than was seen offshore.

Loliginids have been considered to be demersal squids (Bidder, 1968; Zuev and Nesis, 1971; Packard, 1972), but it appears that *Loligo pealei*, in particular, may be more closely associated with the benthos while inshore than had been realized. Offshore it remains on or near the bottom during the day (Serchuk and Rathjen, 1974), but disperses into the water column at night, apparently to feed upon diurnally migrating lanternfishes, euphausids, and mysids (Vovk, 1972; Vinogradov and Noskov, 1979). Peak feeding activity, however, is thought to occur during the day (Vovk, 1972), but benthic or demersal prey are not common in their guts (*op. cit.*). Locally, *L. pealei* has been observed feeding day and night and at the surface or on or near the bottom. Typically adult squid are seen hovering, catching and eating prey, and resting on or near the bottom, and there is some evidence that even hatchlings and small juveniles remain near the bottom particularly during the day (Raytheon, 1978). Gut content analyses which could confirm this hypothesis are lacking for *L. pealei*, but it has been shown that *L. opalescens* does shift to a benthic feeding pattern when it moves onto the Monterey Bay spawning grounds (Karpov and Cailliet, 1978) (Table II).

Feeding and movement patterns

The high incidence of empty guts from inshore (about 53%) is somewhat surprising considering the high metabolic activity of the squid and the rapid growth of young of the year during the summer months. Studies of loliginids indicate that digestion of a meal takes only 2–6 hours (Bidder, 1950; Karpov and Cailliet, 1978; Macy, unpublished), and food consumption rates are also high. Vinogradov and Noskov (1979) estimated that the daily ration of *L. pealei* is only 3.2–3.8% wet weight d^{-1}, but laboratory studies (Macy, 1980) have suggested considerably higher rates of 9–10% d^{-1}, which are comparable to those reported for *L. opalescens* (Karpov and Cailliet, 1978). During the first 6 months after hatching, juvenile squid are thought to grow from 1.0 to over 2.0 cm mo^{-1} (Summers, 1968, 1971; Mesnil, 1977). In light of these data, food supplies must be abundant. Stomach fullness peaks between 1600 and 2000 h daily, and during the summer 90% or more squid may be expected to have food in their guts (Vovk, 1972). Thus inshore feeding activity was probably greatly underestimated in this study because samples were generally taken before noon, prior to highest feeding activity.

During the winter months when squid concentrate in canyon mouths along the continental slope (Summers, 1969; Serchuk and Rathjen, 1974), food supplies may become limiting. Although the overall incidence of squid with empty guts from offshore was only slightly higher than from inshore (55% *vs.* 53%) in the present study, values ranged from 49% to 68% for individual collections within the pooled sample (*e.g.* Cryos 1976, Argus 1977, 1978), which are consistent with other published results. Vovk (1972), for example, found that the incidence of empty guts typically exceeds 60% from November through March offshore, and even during the August-November period, values as high as 54% were reported from the New England continental shelf (Vinogradov and Noskov, 1979). Winter growth rates of only 0.4–0.6 cm mo^{-1} (Mesnil, 1977), presumably reflect lack of food, and it should also be noted that in late spring and early summer even immature juveniles leave the slope waters and move onto "feeding grounds" (Vovk, 1978) further inshore on the shelf.

Loligo pealei is clearly an opportunistic predator, whose highly mobile fish-like mode of existence allows it to effectively utilize a wide variety of potential prey species. In highly productive coastal waters such as Narragansett Bay and Vineyard Sound (Summers, 1968), food resources are plentiful. In the slope regions where squid overwinter, productivity is probably considerably lower. No significant energy storage reserves (other than gonads) have been found in this species either, and thus frequent feeding may be required. Since squid tend to concentrate in the relatively warmer canyon mouths, prey "patch" size and the spacing between patches may be the most important factors which determine whether or not minimum daily metabolic needs are met. Much of the variability in the reported incidence of empty guts offshore must reflect inherent variability (patchiness) in the distribution of prey species. High levels of cannibalism, mainly among larger squid (Table II), may also indicate lack of other suitable prey within an area. Thus, the annual inshore-offshore migrations which *L. pealei* makes north of Cape Hatteras may be more closely related to the need to insure adequate food supplies for reproduction and growth of young than to avoidance of excessive ranges of temperature or salinity (Hixon, 1980; Whittaker, 1980). Temporary local movements into salt ponds and canals, as have been observed are clearly food-oriented.

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